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Metapopulation structure and dynamics of British Columbia herring

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ABSTRACT

The purpose of this exploratory paper is to integrate existing knowledge about the dispersal and population dynamics of the five major BC herring stocks into a structured metapopulation model (SMP). We used the model to quantify the amount of straying that occurred during the 1977-98 base period. Tagging studies indicate that dispersal rates for the five major BC herring populations during this period ranged from 14% to 36% per year, and appeared to be an increasing function of the biomass of the spawning stock in each population. The tagging studies also indicated that the dispersal pattern matched an isolation by distance model. That is, most herring dispersed to nearby populations, but a few strayed to the most distant ones. Consequently, all of the major BC herring populations are genetically linked by dispersal, and the dispersal rates are high enough to ensure that there is unlikely to be any genetic differentiation between the major populations. During the warm ocean climate regime, which prevailed during the base period, the SMP model suggests that about 25 kt/yr of adult herring migrated between the five major populations. The productive Georgia Strait population exported about 12 kt of adults per year to the other four, less productive populations.

The SMP model suggests that dispersal is important because it tends to stabilize the spatial distribution of spawners in the metapopulation and increases the persistence time of the less productive populations in two ways: 1) the density-dependent straying response increases the fidelity rate when the population is declining, and (2) declining populations will tend to receive more migrants from other populations than they export. Dispersal is also important because it recolonizes new and vacant spawning habitat. Conceptually, this enables the metapopulation to "adapt" to habitat changes, and to alter its distribution pattern in response to low frequency trends in climate, and other factors. From a stock forecasting perspective, straying probably has the largest effect on the metapopulation when an exceptionally large year-class recruits to one of the local populations. When this occurs a significant proportion of the resulting adult biomass may be exported to nearby populations, much like a radiating wave which decreases in height as it moves further away from the source population. For example, the SMP model suggested that after the exceptionally large 1977-yr class recruited to the QCI population, about 7 kt of herring might have migrated to the Central Coast population, and a roughly equal amount to the PRD population in both 1980 and 1981. The "unexpected" appearance of this amount of biomass would cause the forecasts for these stocks to be low.

Year-class strength synchrony in several nearby BC herring populations in 1977 and 1985 may have been caused by high juvenile herring survival rates over a large geographical area. However, it might also reflect significant straying by juvenile herring from a source population, which had a locally high juvenile survival rate, to nearby populations. More research needs to be done to measure juvenile herring dispersal rates, and their impact on recruitment in adjacent populations. We stress that the foregoing conclusions only apply to the warm climate regime, which prevailed during the base period analyzed here. The straying dynamics and productivity of BC herring populations during cool climate regimes will be examined in a future PSARC paper.

RÉSUMÉ

Cet article préliminaire a pour objet d'intégrer les connaissances existantes sur la dispersion et la dynamique de la population de cinq principaux stocks de hareng de la C.-B. dans un modèle de métapopulation structurée (MPS-SMP). Nous avons utilisé le modèle pour quantifier le vagabondage qui a eu cours durant la période de référence de 1977-1998. Des études de marquage ont révélé qu'au cours de cette période, les taux de dispersion pour les cinq principales populations de hareng de la C.-B. ont varié entre 14 et 36 % par année et semblaient dépendre de plus en plus de la biomasse du stock reproducteur dans chaque population. Elles ont aussi révélé que le schéma de dispersion correspondait à un modèle d'isolement à cause de la distance. En d'autres mots, la plupart des harengs se sont dispersés vers des populations à proximité, mais quelques-uns ont vagabondé jusqu'aux plus éloignées. Par conséquent, toutes les principales populations de hareng de la C.-B. sont liées sur le plan génétique en raison de la dispersion, et les taux de dispersion sont suffisamment élevés pour assurer qu'une différenciation génétique entre les principales populations soit improbable. Pendant le régime de climat océanique chaud, qui a dominé pendant la période de référence, le modèle de MPS suggère qu'environ 25 kt de harengs adultes par année ont migré entre les cinq principales populations. La population productive du détroit de Georgia a exporté environ 12 kt d'adultes par année vers les quatre autres populations moins productives.

Le modèle de MPS suggère que la dispersion est importante parce qu'elle tend à stabiliser la distribution spatiale des reproducteurs dans la métapopulation et prolonge la persistance des populations moins productives de deux façons : 1) la réaction de vagabondage tributaire de la densité accroît le taux de fidélité lorsque la population est en déclin et 2) les populations en baisse auront tendance à recevoir plus de migrateurs qu'elles n'en perdent par rapport aux autres populations. La dispersion est également importante parce que les vagabonds recolonisent de nouvelles frayères inoccupées. Sur le plan conceptuel, elle permet à la métapopulation de s'adapter aux changements d'habitat et de modifier le modèle de sa distribution en réponse aux tendances peu fréquentes dans le climat et à d'autres facteurs. Du point de vue de la prévision des stocks, le vagabondage exerce probablement l'effet le plus important sur la métapopulation lorsqu'une classe d'âge exceptionnellement importante recrute à l'une des populations locales. Le cas échéant, une proportion significative de la biomasse des adultes résultante peut être exportée aux populations voisines, à l'image d'une onde rayonnante qui diminue de hauteur au fur et à mesure qu'elle s'éloigne de la population source. Par exemple, le modèle de MPS a suggéré qu'après le recrutement de la classe d'âge 1977 exceptionnellement importante à la population QCI, environ 7 kt de harengs pourraient avoir migré vers la population du centre de la côte, et à peu près la même quantité à la population PRD à la fois en 1980 et en 1981. L'apparition « inattendue » de cette quantité de biomasse ferait baisser les prévisions pour ces stocks.

La synchronisation de la vigueur de la classe d'âge dans plusieurs populations de hareng voisines en C.-B. en 1977 et en 1985 pourrait s'expliquer par des taux de survie élevés des juvéniles sur une vaste région géographique. Cependant, elle pourrait aussi refléter un taux de vagabondage important chez les juvéniles d'une population source, qui avaient un

taux de survie élevé à l'échelle locale, vers des populations voisines. D'autres recherches sont nécessaires pour mesurer les taux de dispersion des juvéniles et leur impact sur le recrutement dans des populations adjacentes. Nous insistons sur le fait que les conclusions précédentes ne s'appliquent qu'au régime de climat chaud qui a dominé pendant la période de référence que nous avons analysée. La dynamique du vagabondage et la productivité des populations de hareng de la C.-B. pendant les régimes de climat froid seront examinées dans un prochain article du CEESP.

INTRODUCTION

In the past decade there has been a renewed interest in studying the spatial structure of natural populations, because it is now widely recognized that most animals live and reproduce in fragmented habitats. In this context, McQuinn (1997) reviewed the ecological characteristics of Atlantic and Pacific herring and concluded that the stock structure of these species resembled a *metapopulation*. A metapopulation is simply a set of interacting, local breeding populations, which are linked by dispersal (gene flow). Dispersal is important because it can have a significant effect on the production dynamics and genetic differentiation of local populations. Metapopulation theory also recognizes that some populations can disappear for a time, because of a temporary loss in the amount (or quality) of the spawning habitat, recruitment failure, or simply by chance. However, when suitable conditions return these vacant habitats can be recolonized by strays from nearby populations (Hanski and Simberloff 1997). Extensive research indicates that the spawning habitat of B.C. herring is indeed fragmented, and that herring stray between these fragments both within and between stock assessment regions (Hay et al 1999). Ware et al (2000) reanalyzed a subset of the tagging data for the five, major migratory herring populations in B.C. (Fig. 1). They found that these populations were linked by dispersal, and that the straying pattern matched an isolation by distance model. Although the data are not extensive, the straying rates appeared to increase as the biomass of spawners approached the population carrying capacity (Ware et al 2000).

The purpose of this exploratory analysis is to integrate existing knowledge about the dispersal, and population dynamics of the five major, B.C. herring stocks into a structured metapopulation model (SMP). Models of this form contain an explicit description of the local dynamics of the component populations, and include the effects of dispersal on population growth rates (Hanski 1996). In this paper we develop an SMP model and use it: 1) to quantify the amount of straying that has occurred between the major B.C. herring populations over the last 20 years; 2) to assess the impact of straying on the dynamics of these populations and on their unfished equilibrium levels, which are used to establish the commercial roe fishery reference point; and 3) to evaluate the impact of large year-classes on the dynamics of the metapopulation.

METHODS

Data Sources. Estimated spawner, and age 2+ pre-recruit biomass time series for each population were obtained from age-structured, stock assessment model (ASM) analyses. The version of the ASM that we used assumes that q (the conversion factor relating the estimated egg production of each population to the number of eggs measured by diver surveys on the spawning grounds after 1987) was equal to 1 (see Schweigert 2001). Additional catch, age composition and weight-at-age data were obtained from the Pacific Biological Station herring database. The methods used to estimate the straying rates in this paper and the limitations of the data are outlined in detail in Ware et al (2000).

Metapopulation Model Structure. Five, major migratory herring stocks (populations) (Fig. 1) and a number of minor stocks are currently recognized in BC for management purposes (Schweigert 2001). This paper focuses on the dispersal rates and dynamics of the major populations. The SMP model estimates the prefishery biomass (PFB) of each population just before the roe fishery occurs in the spring. In the model a year begins in March/April of year *t* and ends in March/April of year *t+1*. The model keeps track of the biomass leaving and entering the age 2+ and older component of each population due to: recruitment, fishing, spawning, dispersal (immigration and emigration), growth, and natural mortality. The five local populations are linked in the model by an empirically based distance- and density-dependent dispersal (straying) process. Dispersal is presumed to occur soon after spawning when the adult fish return to the offshore feeding grounds. An isolation by distance relationship is used to describe the straying rate pattern (i.e. where the strays go). Fish, which are imported to other populations are presumed to grow and die at the same rates as the fish in the destination population. The SMP model also contains a partial recruitment scheme. The biomass of age 2+ recruits that join the inshore prefishery biomass in year *t* is determined by a population specific availability factor, which is calculated by the age structured model. In the SMP model, the remaining recruits (R_Recruits) that didn't spawn in year *t* join the repeat spawner pool on the offshore feeding grounds, and spawn in year *t+1*.

The structure of the metapopulation model is illustrated in Fig. 2. The model uses the following notation: j = source population, k = destination population, t = year; and contains the following variables.

- *Prefishery biomass* ($PFB_{j,t}$, kt). Biomass of the adult component (ages 2+ and older) of population *j* on the spawning grounds just before the roe fishery occurs in year *t*.
- *Catch*$_{j,t}$ (kt), the amount of biomass removed from population *j* by the fishery in year *t*.
- *Harvest rate*$_{j,t}$ (HR), defined as $Catch_{j,t}/PFB_{j,t}$.
- *Spawner biomass* ($SB_{j,t}$, kt). Biomass of fish in population *j*, which survive the fishery and spawn ($SB_{j,t} = PFB_{j,t} - Catch_{j,t}$).
- *Spawn*$_{j,t}$ deposited by population *j* in year *t*, calculated as $0.23*SB_{j,t}$ which assumes a 50:50 sex ratio.
- *Adult biomass of population j after spawning* and before straying occurs ($IB_{j,t}$, kt). $IB_{j,t} = SB_{j,t} - Spawn_{j,t}$.
- *Straying rate* ($SR_{j,t}$). Proportion of herring in population *j* that disperse to other populations, according to some user defined function (see below).
- *EXPORT*$_{j,t}$ *(Emigration)*. Biomass of herring that stray from population *j*. $Export_{j,t} = SR_{j,t}*IB_{j,t}$.
- *IMPORT*$_{j,t}$ *(Immigration)*. Biomass of herring that stray to population *j* from the other four populations in year *t*.
- *Population specific instantaneous natural mortality rate* (M_j, yr^{-1})
- *Population specific survival rate*, defined as $\exp(-M_j)$.
- *Population specific adult growth rate* defined as $\exp(G_j)$, where G_j is the instantaneous growth rate.

- *Remaining biomass ($RB_{j,t}$)*. Biomass (kt) of adult herring in population *j* that did not disperse. $RB_{j,t} = IB_{j,t} - Export_{j,t}$.
- *Pre-recruits ($PRB_{j,t}$)*. Biomass of age 2+ herring (kt) in population *j* on the offshore feeding banks in year *t*.
- *$Recruits_{j,t}$*. Biomass of pre-recruits that migrate inshore and enter the prefishery biomass of population *j* on the spawning grounds in year *t*. The proportion of the pre-recruit biomass that joins the $PFB_{j,t}$ is determined by a population-specific *availability factor*$_j$ calculated by the age-structured model. Recruitment occurs with a 3-yr time delay in the model according to some user defined stock-recruitment function (see below), or by a recruitment time series that is output by the age-structured model.
- *Repeat Spawners ($RS_{j,t\ initial}$)*. The initial size of the repeat spawner pool in population *j* at the beginning of the growing season in year *t*: $RS_{j,t\ initial} = RB_{j,t} + R_Recruits_{j,t}$.
- *$R_Recruits_{j,t}$*. These are the remaining pre-recruits, which join the repeat spawner pool of population *j* on the offshore feeding banks after the spawning season in year *t*. They will spawn in year *t+1*. Hence, $R_Recruits_{j,t+1} = (1\text{-}availability_j)*PRB_{j,t}$.

Warm Base Period. The model was applied to a specific period of time (1977 to 1998) called the *base period*. This period was chosen because it encompasses the modern roe fishery, and because ocean conditions were anomalously warm at that time. Previous work indicates that warm ocean conditions have a negative impact on recruitment in the southern B.C. herring populations, particularly the west coast Vancouver Island stock (Ware 1996). In the first part of this paper, average parameter values calculated by the age-structured model for the base period (Table 1) are used to estimate the average dispersal of biomass between the populations, and to calculate a dispersal-adjusted natural mortality rate for each population (see below).

Table 1. Average values estimated from age-structured model output for the warm base period.

Population	PFB_j (kt)	$Catch_j$ (kt)	SB_j (kt)	Pre-recruits$_j$ (kt)	Pre-recruit Availability$_j$	Harvest Rate$_j$
West Coast Vancouver Island (WCVI)	38.8	8.2	30.6	14.2	0.68	0.211
Georgia Strait (GS)	65.5	12.8	52.7	28.6	0.71	0.195
Central Coast (CC)	30.0	7.1	22.9	10.0	0.56	0.237
Queen Charlotte Is. (QCI)	25.7	4.0	21.7	12.5	0.40	0.156
Prince Rupert District (PRD)	28.7	5.2	23.5	11.6	0.48	0.181
Total	188.7	37.3	151.4	76.9		0.198

RESULTS

Density-dependent dispersal. Straying rate data (from Ware et al (2000), Table 2B) for the base period come from tags that were released on, or near, the spawning grounds in 1982, 1989, 1990 and 1991, and were recovered a year later during the spawning period (February to April). The estimated straying rates (in year *t*) ranged from 14 to 36%, and appeared to be a saturating function of the spawner biomass (SB_j in year *t*). The data summarized in Fig. 3 can be adequately described by a logistic function, which rises to a

maximum straying rate of 33% (r^2 between the observed and fitted values = 0.85). One data point for the QCI population (1990 release) was a statistical outlier and was excluded from the analysis. Unfortunately, there are not enough data to determine if the parameter values describing the relationship between the dispersal rate and spawner biomass differ between populations. We suspect that they probably do. However, because this possibility can not be resolved at this time, as an interim measure we have assumed that a common straying relationship can be applied to all the populations:

$$\text{Straying rate}_{j,t} = 0.33/(1+7.09\text{EXP}(-0.0813\ SB_{j,t}) \qquad 1.$$

Distance-Dependent Dispersal Pattern. Ware et al (2000) found that the proportion of strays recovered for each population decreased with the degree of separation between the release (source population, *j*) and recovery (destination population, *k*) sites (Table 2).

Table 2. Distances (km) between the the geographical centers of each population. These are the shortest distances that fish could migrate between populations without traversing major land masses.

	$WCVI_k$	GS_k	CC_k	QCI_k	PRD_k
$WCVI_j$	•	274	447	596	713
GS_j	274	•	434	622	776
CC_j	447	434	•	202	303
QCI_j	596	622	202	•	197
PRD_j	713	776	303	197	•

The proportion ($P_{j,k}$) of strays migrating from population *j* to population *k* in year *t* declined exponentially with the distance ($D_{j,k}$, km) between populations (Fig.4):

$$P_{j,k} = 0.75 \exp(-0.003\ D_{j,k}) \qquad 2.$$

Equation 2 was used to compute the dispersal pattern ($P_{j,k}$) for each population during the base period (Table 3).

Table 3. Base period dispersal pattern from source population *j* to destination population *k* derived from eq. 2. The relative proportions calculated from eq. 2 were normalized so the proportion of strays exported from each population to the other four populations was equal to 1. This normalization procedure causes the dispersal pattern matrix to become slightly asymmetrical, because the *average* distance between the source population and the other four populations is different for each source (see Table 2). For example, the average distance between the QCI population and the other four populations is 346 km, while the average distance between the Georgia Strait population and the other populations is much larger (524 km). These differences cause the dispersal matrix to be asymmetrical.

	$WCVI_k$	GS_k	CC_k	QCI_k	PRD_k
$WCVI_j$	.	0.446	0.265	0.169	0.119
GS_j	0.456	.	0.282	0.160	0.101
CC_j	0.176	0.184	.	0.368	0.272
QCI_j	0.117	0.109	0.384	.	0.390
PRD_j	0.100	0.083	0.344	0.473	.

Warm Base Period Dispersal. Output data from the age-structured model (Table 1), the density-dependent straying rate function (eq. 1) and the isolation by distance dispersal

pattern (Table 3) were used to calculate the average dispersal rates from each population during the base period (Table 4).

Table 4. Estimated average dispersal of age 2+ (and older) biomass (kt/yr) from source population *j* to destination population *k* during the base period. The row totals indicate the total biomass exported from the source population in that row. While the column totals indicate the total biomass imported to the destination population in that column.

Population	$WCVI_k$	GS_k	CC_k	QCI_k	PRD_k	Total Export
$WCVI_j$	.	2.06	1.31	0.96	0.57	4.90
GS_j	5.55	.	3.73	1.81	1.11	12.20
CC_j	0.55	0.46	.	1.01	0.79	2.81
QCI_j	0.25	0.28	1.02	.	0.92	2.47
PRD_j	0.29	0.26	0.97	1.43	.	2.95
Total Import	6.59	3.06	7.03	5.21	3.36	25.33

Adult Growth and Mortality Rates. Population-specific instantaneous growth rates (G_j) were estimated by weighting the average age-specific instantaneous growth rates for the base period by the available proportion of mature fish at each age in the population.

The population-specific natural mortality rates (M_j) estimated by the age-structured model are actually *net loss rates*, which include real natural mortality plus the "hidden" effects of immigration and emigration. Therefore, we calculated an adjusted-M (M_j) to account for the dispersal from, and to, each population. For mass balance, it follows that the PFB_j at the end of year *t* is equal to the recruiting biomass of age 2+ fish, plus the biomass of repeat spawners ($RS_{j,t}$) plus the imported biomass ($IMPORT_{j,t}$) of mature fish in year *t*. Thus,

$$PFB_{j,t} = [Availability_j * Pre\text{-}recruits_{j,t}] + (RS_{j,t} + IMPORT_{j,t})_{final} \qquad 3.$$

We calculated the average, initial biomass of repeat spawners and imported adults during the base period $(RS_{j,t}+IMPORT_{j,t})_{initial}$ from the age-structured model output and the estimated dispersal rates (Table 4). The biomass of repeat spawners and imported adults $(RS_{j,t} + IMPORT_{j,t})_{final}$ at the end of year *t* after all the growth and natural mortality has occurred is given by:

$$(RS_{j,t}+IMPORT_{j,t})_{final} = (RS_{j,t}+IMPORT_{j,t})_{initial} EXP(G_j-M_j) \qquad 4.$$

Equation 4 was then rearranged to yield a dispersal-adjusted natural mortality rate (M_j) for each population:

$$M_j = \ln [(RS_{j,k} + IMPORT_{j,k})_{final} / (RS_{j,k}+IMPORT_{j,k})_{initial}] - G_j \qquad 5.$$

The results are summarized in Table 5.

Table.5. Population-specific average adult growth rates (G_j), age-structured model net loss rates, (ASM-M_j) and dispersal-adjusted natural mortality rates (M_j) during the base period.

Population	G_j (yr^{-1})	ASM-M_j	M_j (yr^{-1})
WCVI	0.479	-0.444	-0.501
GS	0.460	-0.539	-0.332
CC	0.379	-0.278	-0.453
QCI	0.344	-0.500	-0.608
PRD	0.355	-0.379	-0.424
Average	0.403	-0.428	-0.464

Recruitment. To estimate the unfished equilibrium biomass we require a stock-recruitment relationship, which describes how recruitment changes with variations in spawner biomass. Instead of approaching the data with a preconceived idea of what the underlying relationship was, we plotted the pre-recruit biomass in yr $t+3$ against the parent spawner biomass in yr t. The resulting scatterplots were then smoothed by a distance weighted least squares regression (DWLS, Systat). This regression procedure fits a line through a set of points by least squares. However, unlike linear or low order polynomial smoothing, the surface is allowed to flex locally to fit the data better. This method produces a true, locally weighted curve, where data points far from a selected point contribute little to the prediction and data points near contribute the most (Wilkinson et al 1996). The DWLS analysis indicated that the underlying relationship between recruitment (PRB_j) and parent stock biomass (SB_j) resembled either the well-known Ricker curve, or a "hockey stick" relationship. Barrowman and Myers (2000) examined the properties of the hockey stick and Beverton-Holt models. They found that the hockey stick model usually gave a lower estimate of the slope at the origin than the Beverton-Holt model. Accordingly, the latter model tends to overestimate the resilience of a population to fishing, and its carrying capacity compared with the hockey stick model. For these reasons, we considered the hockey stick model to be more appropriate in this case than the Beverton-Holt relationship, even though both models might fit a noisy set of data equally well.

In the hockey stick model, recruitment increases linearly with SB_j until the latter reaches a threshold biomass (TSB_j). *Above the TSB, recruitment becomes independent of the size of the parent stock with a relatively large random lognormal variance.* This means that most yr-classes are of below average strength but occasionally a combination of very favorable conditions produces an exceptionally large yr-class. An important difference between the Ricker and hockey stick models is that recruitment declines at high parent stock biomasses in the Ricker model, while in the hockey stick model it doesn't.

Warm Base Period Stock-Recruitment Relationships. Because the average biomass of age 2+ herring that recruit to the three southern populations tends to be lower during warm climate regimes, we stress that the stock-recruitment relationships described below (and in Table 6) only apply to the 1977-98 base period. They are not applicable during cool climate regimes, and they may not even be applicable during future warm regimes, if the predator-prey interactions that affect herring recruitment change.

WCVI Population. The base period recruitment data fit a hockey stick model (Fig.5). For the density-dependent phase of the relationship. i.e. when SB < 18 kt, the biomass of pre-

recruits increased linearly with SB. For the density-independent phase, i.e. when SB>20 kt the pre-recruit biomass (PRB) averaged 13.8 kt, the median was 11.0 kt and the variance/mean ratio was 11.1. For comparison, the average biomass of pre-recruits in the WCVI population was about 2.2x larger during the cool ocean regime conditions between 1950 to 1976.

Georgia Strait Population. The base period recruitment data fit a hockey stick model (Fig.5). For the density-dependent phase of the relationship, when SB < 20 kt the pre-recruit biomass increased linearly with SB. For SB>20 kt, the pre-recruit biomass was independent of SB, and averaged 28.4 kt, the median PRB was 27.2 and the variance/mean ratio was 6.4. Average recruitment in this population was slightly larger (about 1.2x) during the cool regime between 1950 to 1976.

Central Coast Population. The base period recruitment data fit a hockey stick model (Fig.5). For the density-dependent phase of the relationship, when SB <15 kt pre-recruit biomass increased linearly with SB. For SB>15 kt, pre-recruit biomass was independent of SB, and averaged 11.0 kt, the median PRB was 6.6 kt and the variance/mean ratio was 13.7. Average recruitment in this population was about 1.5x larger during the cool regime between 1950 to 1976.

Queen Charlotte Islands Population. The base period recruitment data fit a hockey stick model (Fig.5). However, the relationship in this case is noisier and the location of the threshold spawner biomass is more uncertain. We assumed it was around 15kt. When the SB>15 kt, pre-recruit biomass was independent of SB, and averaged 9.3 kt, the median PRB was 6.6 kt, and the variance/mean ratio was 10.0. The extraordinarily large 1977 yr-class (about 110 kt) is not shown, and was not included in the stock-recruit analysis, because it was such an extreme outlier. Including it would have biased the results by making this population appear to be more productive than it is. In contrast to the three southern stocks, the average recruitment in this population was *slightly larger* (1.1x) during the warm base period than it was during the 1950 to 1976 cool regime.

Prince Rupert District Population. The DWLS analysis indicated that the base period recruitment data for the prince Rupert stock was dome-shaped (Fig. 5). So the data were fit to a Ricker model. In this case, the maximum biomass of pre-recruits (about 11.1 kt) is produced by a spawner biomass of about 20 kt. Average recruitment in this population was *larger* (about 1.3x) during the warm base period than it was during the 1950 to 1976 cool regime. We used the Ricker model for this population because the data clearly indicate a declining trend in recruit biomass with high parent biomass, which may have a biological basis. For example, if the spawning habitat of this population is more limited a higher spawner biomass may result in higher egg mortality rates. Alternatively, the PRD adults might remain near the spawning area to forage after the eggs have hatched. This could cause a higher larval mortality rate when the parent stock is large. During the base period the mean recruitment to this population was 12.6 kt, the median was 9.0 kt and the variance to mean ratio was 6.8.

Table 6. Summary of stock-recruitment parameters for the warm base period. The last column indicates the median pre-recruit biomass (PRB_j) above the threshold TSB_j. For the hockey stick function, Barrowman and Myers (2000) recommend using the median recruitment when the spawner biomass exceeds the TSB.

Stock	Function	Threshold SB (TSB, kt)	Slope	Median PRB (kt)
WCVI	Hockey stick	20	0.55	11.0
GS	Hockey stick	20	1.36	27.2
CC	Hockey stick	15	0.48	7.2
QCI	Hockey stick	15	0.44	6.6
PRD	Ricker PRB = 1.92SB EXP(-0.062 SB)	.	.	9.0

Unfished Equilibrium Biomass (SBK_j). The theoretical unfished carrying capacity of a population is determined by all the processes, which annually add and remove biomass from the population. At equilibrium, the addition of new biomass from recruitment, growth and straying (import) equals the losses removed by spawning, export, and natural mortality. The unfished equilibrium spawner biomass (SBK_j) during the base period was estimated by: 1) setting the harvest rate to 0; and 2) applying the population-specific warm base period stock-recruit relationship (Table 6), the adjusted natural mortality rate (Table 5); 4), the common straying rate function (eq. 1); and the isolation by distance dispersal rates (Table 3). The results are summarized in Table 7.

Table 7. Estimated unfished equilibrium spawner biomass (SBK_j) for the warm base period. The biomass (kt) that is exported (E_j) and imported (I_j) annually to each population at equilibrium is indicated. I_j-E_j indicates the net effect of dispersal in each case.

Population	SBK_j (kt)	$Export_j$	$Import_j$	I_j-E_j
WCVI	49	11	13	2
GS	86	22	7	-15
CC	40	8	13	5
QCI	27	4	11	7
PRD	33	6	7	1
Total (kt)	235	51	51	0

Taking the average base period PFB_js as the starting point for the simulation, the populations required about 9 years to reach equilibrium once the harvest rate was removed. The resulting theoretical unfished equilibrium biomass of the metapopulation during the warm base period is estimated to be about 235,000 t. At equilibrium roughly 51,000 t of mature herring will disperse through the metapopulation annually. The difference between the imported and exported biomass in Table 7 illustrates that the most productive population (Georgia Strait) is a net exporter of adult herring, while the other four populations are net importers, particularly the Central Coast and QCI populations. Consequently, the dispersal process tends to stabilize the spatial distribution of herring in the metapopulation by moving individuals from more productive populations to less productive ones. During warm climate regimes, this stabilizing influence, in both the unfished and fished states, appears to be provided exclusively by the Georgia Strait population.

We also examined the influence of a large (50%) random variation in the straying rate in each population on the unfished equilibrium biomass. The results (Fig. 6) indicate that

random variations in straying rates cause the populations to fluctuate about the same carrying capacities (SBK_j) as they did in the deterministic case (Table 7). In other words, random variations in straying rates will affect the time-evolving dynamics of the populations, but did not affect their *average* unfished equilibrium biomass.

The Cutoff reference point for each population, is defined as 25% of the unfished equilibrium biomass. According to current management practice, when a population falls below its Cutoff the commercial roe fishery is terminated to allow the local spawner biomass to rebuild. *Because the Cutoff is intended to be a precautionary limit reference point, which conserves the productivity of each stock, this reference point should be estimated during climate regimes when the populations are most productive.* As noted above, since the productivity of the three southern populations (WCVI, GS and CC) was lower during the warm base period, we recommend that the Cutoffs currently being used by PSARC be retained until cool regime unfished equilibrium levels are estimated from the historical data. The appropriate Cutoff levels can then be re-evaluated for each population.

Dispersal Waves Caused by Large Year-classes. The density-dependent relationship between the straying rate and spawner biomass, and the isolation by distance dispersal pattern imply that straying will have the greatest effect on the metapopulation when a large year-class appears in one of the local populations. To evaluate the potential implications we simulated what may have happened when the exceptionally large 1977 year class recruited to the QCI population. To parameterize the SMP model we used the common straying rate relationship (eq.2), and the population-specific base period: recruitment, harvest, adjusted-natural mortality, and growth rates. The model was run for 15 years to allow the five populations to reach their respective equilibrium PFBs. In the simulation, a recruitment "spike" of 110 kt, which is equivalent to the size of the 1977 year class was introduced to the QCI population in 1977. This year-class recruited to the QCI PFB in 1980 and 1981. Because straying in year t affects the pre-fishery and spawner biomass of nearby populations in the following year ($t+1$), the initial impact of straying from the QCI population appeared in the Central Coast and Prince Rupert District populations in 1981 and 1982 (Table 8).

Table 8. Simulated effect of the anomalously large 1977 QCI year-class on the straying rates in each population.

Year	QCI	CC	PRD	GS	WCVI
1978	0.15	0.16	0.16	0.30	0.21
1979	0.15	0.16	0.16	0.30	0.21
1980	**0.30**	0.16	0.16	0.30	0.21
1981	**0.32**	**0.18**	**0.18**	0.30	0.21
1982	**0.24**	**0.19**	**0.20**	0.30	0.21
1983	**0.18**	**0.18**	**0.18**	0.30	0.21
1984	**0.16**	**0.17**	**0.17**	0.30	0.21
1985	**0.16**	0.16	**0.17**	0.30	0.21

Table 8 indicates that the straying rate from the QCI population may have doubled in 1980 and 1981 and remained above the equilibrium base rate (15%) until 1986. The

resulting increase in dispersal from QCI caused by the 1977 year-class increased the biomass of the CC and PRD populations, and caused their straying rates to rise between 1981 to 1985. During this period, these three populations were passing biomass back and forth. In fact, the simulation suggests that the QCI 1977 yr-class set up a dispersal wave which rippled through the metapopulation for about six years (Fig. 7). The wave peaked in 1981 and then died out as the size of the 1977 yr-class was depleted by natural and fishing mortality. Between 1980 to 1985, the QCI population may have exported an additional 32 kt (above its equilibrium export rate): 13 kt may have dispersed to the CC, 12 kt to the PRD, 4 kt to GS and 3 kt to the WCVI. The biomass imported to the WCVI and GS populations from QCI was relatively small, which explains why there was no measurable increase in the straying rates in these populations (Table 8).

To see if the 'observed' changes in the prefishery biomass in the CC and PRD between 1980 to 1985 contained the "signature" of a dispersal wave originating in QCI, we compared the SMP simulation results with age-structured model estimates of the prefishery biomass in these populations. Clearly, we would not expect an exact match in the rates of increase and decrease in the biomass of these populations, because the SMP model assumes constant recruitment and growth rates, while the ASM uses time-varying rates. Nevertheless there are some similarities worth noting. For example, we found that the general pattern of increase in the CC population following the recruitment of the 1977 year-class in QCI was of the same order as the pattern suggested by the simulation. For example, ASM estimates of the prefishery biomass in the CC population between 1981 to 1984, indicate that it rose an average of 7 kt in both 1981 and 1982, which is of the same order as the 4 kt/yr rise suggested by the simulation. After 1982 the simulation suggested that the CC PFB should have declined about 2 kt/yr for the next two years. This is of the same order as the 7kt/yr decline estimated by the ASM. In the PRD population, the ASM prefishery biomass increased 11 kt between 1981 and 1982, which is similar to the 7kt increase suggested by the simulation. However, due to a local increase in recruitment, which was not included in the SMP model, the PRD population rose slightly in 1983 and again in 1984.

DISCUSSION

The metapopulation model described above incorporates the current extent of our knowledge about the dispersal process in B.C. herring. The model contains two important functional relationships: a density-dependent straying rate, and an isolation by distance straying pattern. Density-dependent dispersal has been observed in other animal populations (Burgman et al 1996). However, we are not aware of any other herring studies, which have reported increases in straying rates with population size. Probably because the extensive, multi-year tagging programs required to obtain such data have not been conducted. Olivieri and Gouyon (1997) considered why dispersal may have evolved. Overall, they noted that there exists a selection for residency within each local population. However, there are factors like avoidance of sib competition and more favorable conditions elsewhere that will select for migration. Dispersal should be favored when there is significant variability in the size of nearby populations. The global

persistence of any genotype requires colonization after local extinction. Olivieri and Gouyon argue that, given enough time, local populations will eventually go extinct, so only genotypes that have migrated will be able to reproduce and persist. Hence, while there may be short-term disadvantages to migration, there may be significant long-term benefits. Expanding on these arguments, we believe there is a selective advantage for the dispersal rate to increase as the spawning and juvenile rearing habitat becomes more crowded. Pacific herring populations in BC have high natural mortality rates (averaging about 0.46 yr^{-1}), so their expected reproductive lifespan is only a few years. When the biomass of a population approaches its carrying capacity, the underlying spawner-recruitment curve causes a sharp decline in the recruits produced by each spawner. Consequently, as the number of spawners increases it may be advantageous for a higher proportion of them to disperse after spawning. Simply by chance, some of these migrants will join populations that are smaller (relative to their carrying capacity), and may produce more recruits over their short reproductive lifespans then the spawners that stayed in the source population. Conversely, there will be a strong selection for residency in a declining population because, all else being equal, each spawner should be able to produce more recruits, due to an improvement in the quality of the spawning and juvenile rearing habitats. A new coded wire tagging program for B.C. herring was initiated in 1999 (Schweigert and Flostrand 2000). A principal objective of this program should be to determine if the straying rate is density-dependent as the existing (but limited) data suggest; and if the straying rate function is population-specific, or if it can be described by a common function.

Studies of natural populations have found that dispersal tends to be higher between populations that are geographically close, and that the decline in the dispersal rate with distance can be described by a negative exponential function (Burgman et al 1996). After analyzing B.C. herring tagging data collected between 1936 to 1951, Taylor (1964) observed that mixing was "greatest between adjacent populations and became less between those farther apart". Ware et al (2000) found the same relationship in tag release and recovery data collected three decades later, during the 1980s. Consequently, an isolation by distance straying pattern appears to be a persistent ecological characteristic of B.C. herring. Mixing between the WCVI and Georgia Strait populations probably occurs on the feeding grounds on the continental shelf off southwest Vancouver Island. Similarly, Central Coast, Georgia Strait, WCVI, and QCI herring probably mix around the Goose Island Bank in Queen Charlotte Sound in the summer. While PRD, CC and QCI herring may be mixing in summer feeding areas in Hecate Strait. Another high-priority objective of the coded wire tagging program should be to determine if the isolation by distance straying pattern shown in Fig. 4 is relatively robust, or if it changes in response to low frequency variations in environmental conditions.

One weakness of our model is that it only accounts for the dispersal of adults. Some data suggest that juvenile herring (i.e. ages 0+,1+ and 2+) may have a higher tendency to stray than the adults (Hourston 1959). We didn't include this component in the SMP model because other than Hourston's observation, nothing is known about the dispersal of juveniles. This is one aspect of herring ecology that requires more research. It is important, because a significant number of fish that recruit to a population may have been

born in nearby populations. Consequently, the phenomenon of year-class synchrony, where adjacent stocks tend to have large year-classes at the same time, may be partly related to increased juvenile migration from a source population, which produced an anomalously large year-class. For example, the 1977 year-class in the QCI, CC and PRD populations, may have been caused in part by a significant dispersal of juveniles from the QCI to the CC and PRD populations

We suspect that the dispersal pattern shown in Table 3 will change in response to protracted temporal and spatial declines in local growth and juvenile survival rates in the metapopulation. Poorer growth and survival rates could be caused by local declines in the abundance of herring prey, and by increases in the abundance of herring predators in the ecosystem. For example, we performed a simple experiment to see how well the SMP model was able to fit the age-structured model output for the latter half of the warm base period (1988-99). We found that the fit was reasonable, but in the SMP model the WCVI and QCI populations were larger than we expected. Three factors could be responsible for this: 1) the natural mortality rates in these populations may have increased; 2) the straying rates may have increased; or 3) the dispersal pattern may have changed, so less strays went to the QCI and WCVI populations during the last half of the base period. We calculated total mortality rates (Z) from the age composition data and fishing mortality rates (F), and could find no evidence that the natural mortality rates (M = Z-F) were significantly different during the first and last halves of the base period in either population. So M doesn't appear to have changed. We also estimated how much the straying rates would have to increase in the WCVI and QCI populations to match the age-structured model output, and found that the required rates were unbelievably high. Finally, we performed an experiment to see if a change in the dispersal pattern could have been responsible. *We found that a decrease in the dispersal of herring to the QCI and WCVI populations in the latter half of the base period provided the best fit to the AS model output.* These results suggest that the much reduced size of the WCVI and QCI populations in the 1990s may have been caused, in part, by a reduction in the amount of herring straying to these populations from the GS, CC and PRD populations shortly after the 1991/92 ENSO, which was followed by a protracted, anomalously warm period.

The model experiments described above clearly highlight the fact that dispersal is a complex process, which probably responds to year-to-year and lower frequency changes in environmental conditions, and other factors that we don't understand yet. Fortunately, the data that will emerge from the new coded wire tagging program can be used to identify other important factors that modify the dispersal rates between B.C. herring populations, and to test the veracity of the density- and distance-dependent straying relationships described in this paper.

CONCLUSIONS

1. The high observed fidelity rates during the warm base period (86% to 64%) provide the biological basis for managing B.C. herring stocks, because it ensures that most of the adult herring that spawn in a specific stock assessment region will return to the same region to spawn the following year.

2. Dispersal rates from the five major populations during the base period ranged from 14% to 36% per year, and appeared to be an increasing function of the biomass of the spawning stock in each population. The new coded wire tagging program should test the generality of this relationship.

3. The dispersal pattern matches an *isolation by distance* model. That is, most herring stray to nearby populations, but a few stray to the most distant ones. Consequently, all of the major B.C. herring populations are genetically linked by dispersal, and the dispersal rates are high enough to ensure that there is unlikely to be any genetic differentiation between them. However, there could be some differentiation in several minor herring populations that are more geographically, or reproductively isolated from the major stocks.

4. During the warm ocean climate regime, which prevailed between 1977-99, about 25 kt/yr of adult herring migrated between the five major populations. The productive Georgia Strait population exported about 12,000 t of adults per year to the other four, less productive stocks. The major beneficiaries were the Central Coast and QCI populations.

5. Dispersal is an important process because it tends to stabilize the spatial distribution of spawners in the metapopulation, and increases the persistence time of the less productive populations in two ways: 1) the density-dependent straying response increases the fidelity rate when a population is declining; and (2) declining populations will tend to receive more migrants from other populations than they export.

6. Dispersal is also important because it recolonizes new and vacant spawning habitat. This enables the metapopulation to adapt to habitat changes, and to alter its spatial distribution in response to low frequency trends in climate, and other factors.

7. From a stock forecasting perspective, straying probably has the largest effect when an exceptionally large year-class appears somewhere in the metapopulation. When this occurs a significant proportion of the recruits may be exported to nearby populations, much like a radiating wave which decreases in height as it moves further away from the source population. For example, after the exceptionally large 1977-yr class recruited to the QCI population, about 7 kt of herring may have migrated in 1980 and again in 1981 to the Central Coast and PRD populations. The

"sudden" appearance of this amount of biomass would cause the stock forecast for these populations to be low.

8. Year-class strength synchrony in several nearby populations in 1985 and 1977 may have been caused by high juvenile survival rates over a large geographical area. However, it could also reflect higher straying by juvenile herring to nearby populations from a source population, which had a locally high juvenile survival. More research needs to be done to measure juvenile herring dispersal rates, and their impact on recruitment in adjacent populations.

9. We stress that the foregoing conclusions only apply to the warm base period analyzed here. We propose to examine how the straying dynamics and productivity of B.C. herring populations change during cool climate regimes in a future PSARC paper.

ACKNOWLEDGEMENTS

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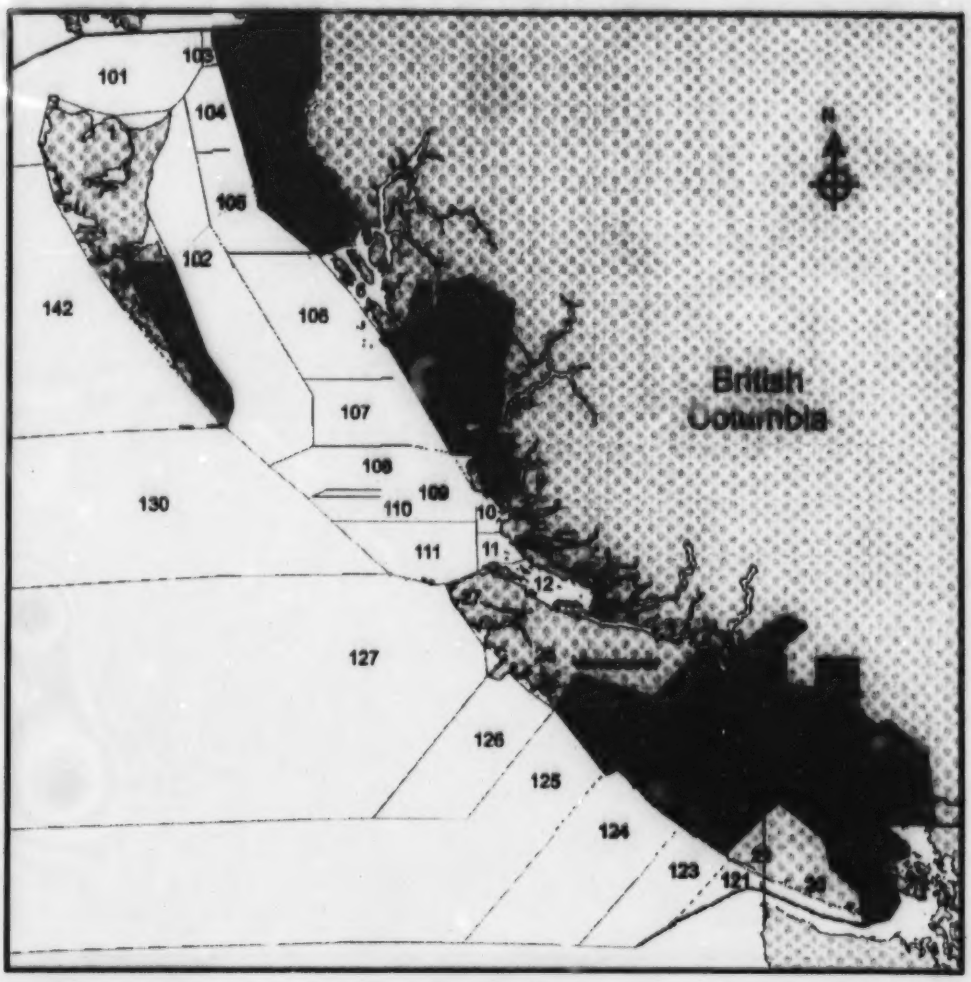


Figure 1. Five major migratory herring populations in British Columbia. West Coast Vancouver Island (WCVI, includes statistical areas 23 to 25), Georgia Strait (GS, includes statistical areas 13 to 29), Central Coast (CC, includes statistical areas 7 to 9); Queen Charlotte Islands (QCI, includes the southeast coast of QCI), Prince Rupert District (PRD, includes statistical areas 3 to 5).

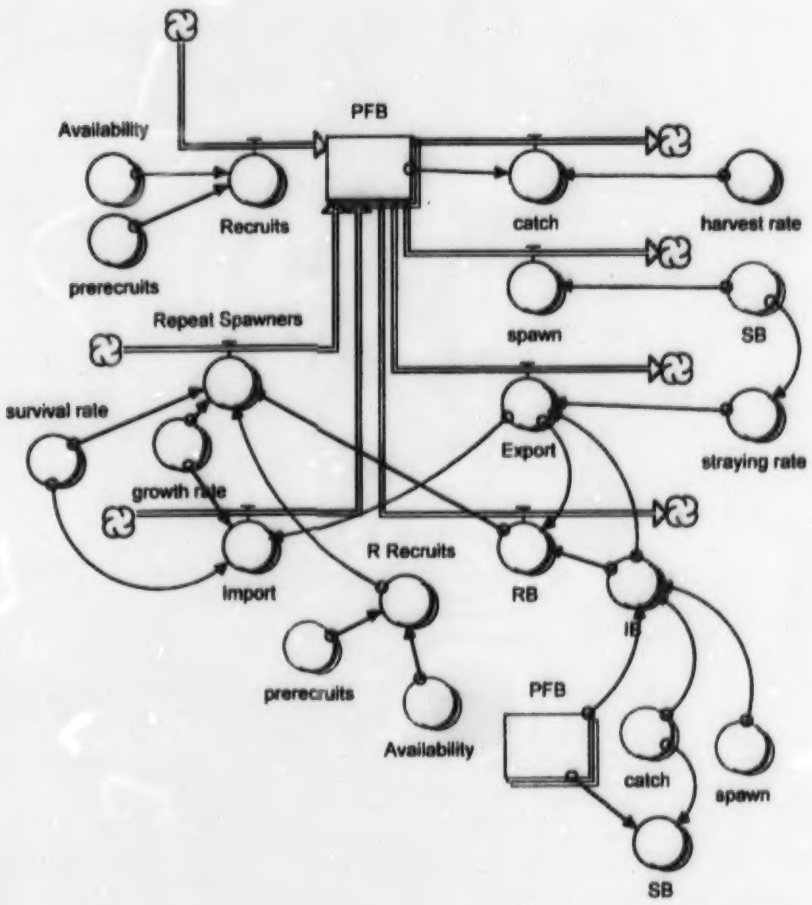


Figure 2. Structured metapopulation model. See text for a description of the variables and process equations.

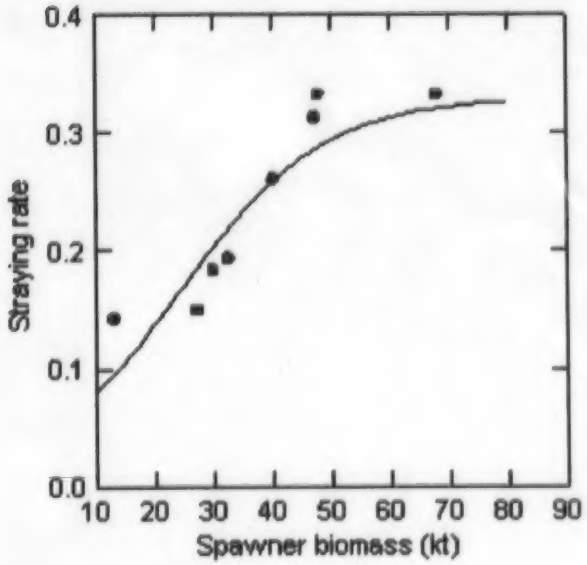


Figure 3. Apparent density-dependent relationship between the biomass of spawners and the straying rate (both in year *t*) during the base period. The data were fit to a logistic function.

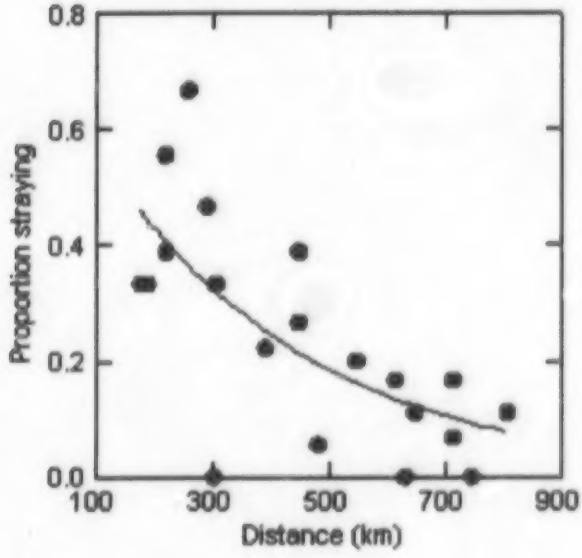


Figure 4. Isolation by distance relationship for B.C. herring during the base period. The points indicate the proportion of herring straying to other populations during one year at large as a function of the distance between the source and destination populations. The data indicate that roughly 41% of the herring that strayed were recovered a year later in adjacent populations that were about 200 km away.

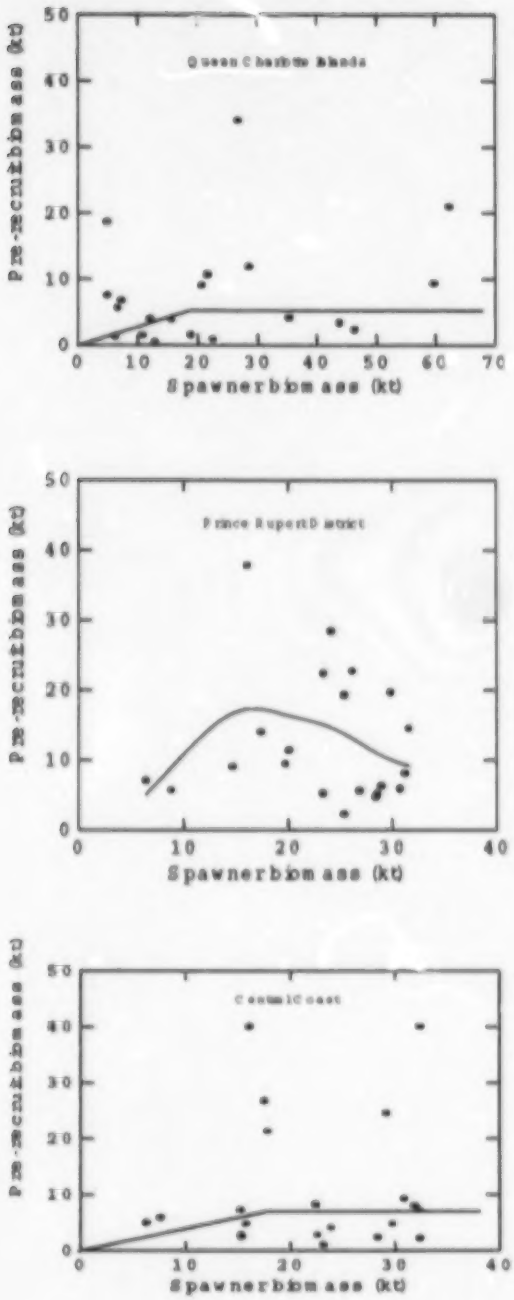
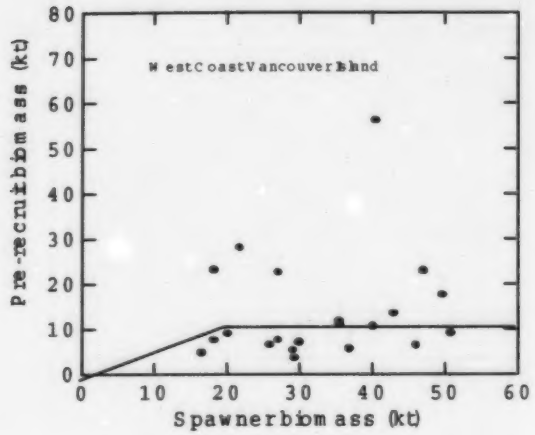


Figure 5. Warm base period stock-recruitment relationships for the five major B.C. herring populations.



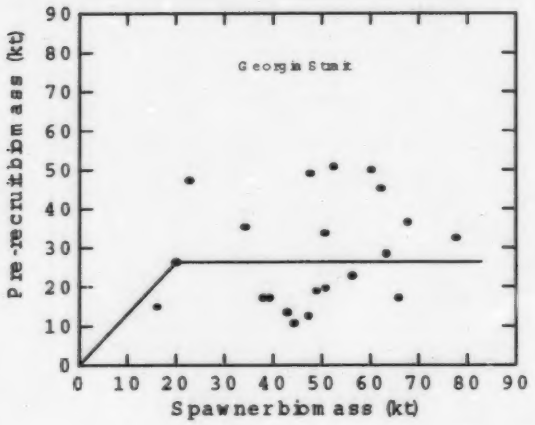


Figure 5. Warm base period stock-recruitment relationships for the five major B.C. herring populations.

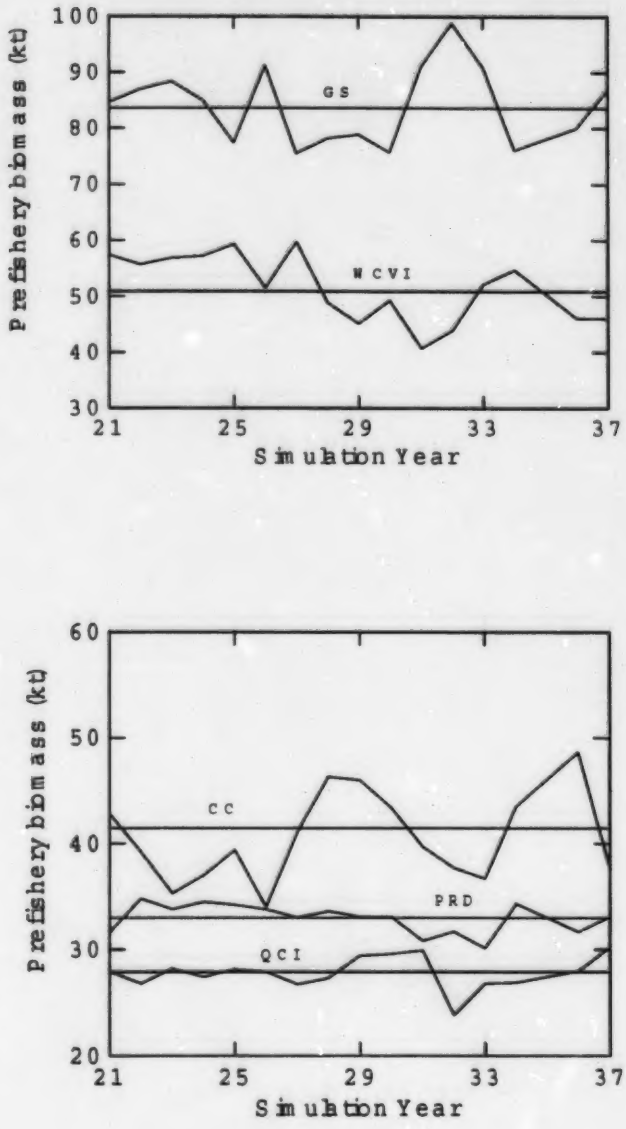


Figure 6. Simulated change in the prefishery biomass in each population assuming a 50% random variation in the annual straying rate. The horizontal lines indicate the average unfished biomass in each case.

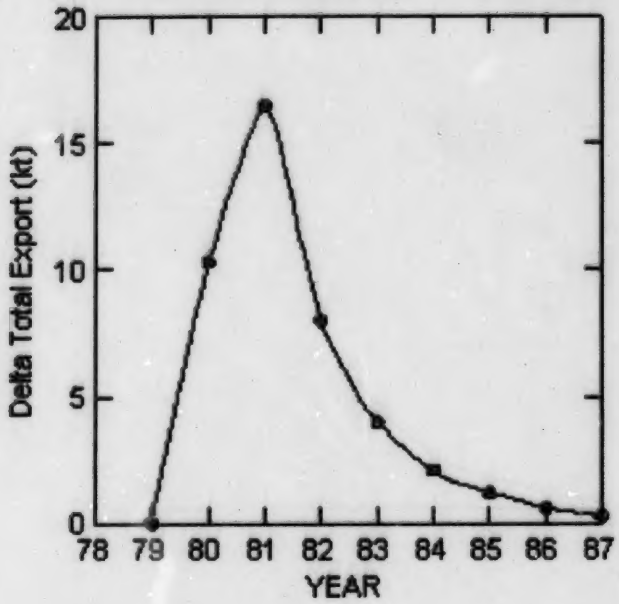


Figure 7. Dispersal wave caused by the anomalously large 1977 year-class when it recruited to the Queen Charlotte Islands population in 1980 and 1981. Delta-Total export represents the additional increase in exported biomass in the metapopulation (above the base level). The dispersal wave lasts for about 6 years, until it is depleted by natural and fishing mortality.